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LETTER

The fossil record of the sixth extinction

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Abstract

Comparing the magnitude of the current biodiversity crisis with those in the fossil record is difficult without an understanding of differential preservation. Integrating data from palaeontological databases with information on IUCN status, ecology and life history characteristics of contemporary mammals, we demonstrate that only a small and biased fraction of threatened species (< 9%) have a fossil record, compared with 20% of non-threatened species. We find strong taphonomic biases related to body size and geographic range. Modern species with a fossil record tend to be large and widespread and were described in the 19th century. The expected magnitude of the current extinction based only on species with a fossil record is about half of that of one based on all modern species; values for genera are similar. The record of ancient extinctions may be similarly biased, with many species having originated and gone extinct without leaving a tangible record.

Keywords

Body size, extinction, fossils, mammals, range, taphonomy.

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INTRODUCTION

The ongoing anthropogenic decline in biodiversity has been dubbed the 'Sixth Extinction' (Leakey & Lewin 1995; Eldredge 1999; Pimm & Brooks 2000; Barnosky *et al*. 2011; Kolbert 2014), in line with the five major mass extinctions commonly recognised in the fossil record (Raup & Sepkoski 1982). Major efforts have been made to compare the scale of the current extinction episode, which is primarily based on terrestrial vertebrates, to those in the fossil record that are largely calculated using shelled marine invertebrate genera (Harnik *et al*. 2012; Finnegan *et al*. 2015), but direct data comparison remains difficult (Barnosky *et al*. 2011; Pimm *et al*. 2014; De Vos *et al*. 2015). Studies of past terrestrial vertebrate extinctions have also mainly focused on fossil genera (Alroy 1996; Barnosky *et al*. 2011; Tomiya 2013; Pimm *et al*. 2014), although a few attempts have been made to estimate species-level rates (Alroy 1999). The scales of extinctions are based on some metric of magnitude (percentage of taxa going extinct) and rate (number of extinctions over some time period) (Barnosky *et al*. 2011). A frequently used metric for comparison has been extinctions per million species-years (E/MSY). A value of 1 E/MSY was originally suggested as the background rate for terrestrial vertebrates based on the fossil record (Pimm *et al*. 1995); a value of 1.8 E/MSY for mammals was given by Barnosky *et al*. (2011) and rounded to 2.0 E/MSY by Ceballos *et al*. (2015). A much lower estimate of about 0.1 E/MSY is based on molecular-based phylogenies and net diversification rates (Pimm *et al*. 2014; De Vos *et al*. 2015).

Meaningful comparisons of magnitude, rate, ecological and taxonomic structure, and potential causal mechanisms of the modern extinction with those in the past depend on the development of compatible data. Specifically, it has been recognised that extinction susceptibility among modern mammals is related to their body size, local abundance and geographic distribution (Alroy 1999; Barnosky *et al*. 2011; Pimm *et al*. 2014) although the relationship with body mass is less clear for earlier mammal extinctions, other than the Late Pleistocene (Alroy 1999; Tomiya 2013). These same factors impact the preservation potential of these animals; that is, to a first approximation larger, more widely distributed and locally abundant mammals should have a higher probability of being recovered as fossils (Behrensmeyer & Chapman 1993; Liow *et al*. 2008). For example, the death assemblage at Amboseli, Kenya has a body size distribution with a larger mean and median than is typical of the live mammal community (Miller *et al*. 2014).

Here, we estimate number of extinctions and standing crop for modern species corrected for differential preservation to compare with magnitudes calculated for ancient extinctions. We do so by examining the number and properties of modern species with or without a current published fossil record (Schopf 1978; Valentine *et al*. 2006). Comparing the known fossil records of threatened and non-threatened modern species clearly demonstrates that those more likely to go extinct in the near future are under-represented. We also assess how characteristics that affect species preservation potentials influence their representation in the record and the resulting estimates of extinction magnitudes.

METHODS

A list of modern mammal species was downloaded from the IUCN Red List of Threatened Species™ on June 26, 2015 (IUCN 2014). It consisted of 5515 species belonging to 1250

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genera. We classified modern and recently extinct mammal species as either 'threatened' or 'not-threatened'; threatened meant it belonged to the Red List categories Extinct (EX; 77 species), Extinct in the Wild (EW; 2 species), Critically Endangered (CR; 212 species) or Endangered (EN; 482 species). The 769 mammal species in these categories belonged to 371 genera. We considered these to be 'extinct in the future.' The remaining 3945 'not threatened' species belonged to the categories Least Concern (LC; 3115 species), Vulnerable (VU; 506 species) and Near Threatened (NT; 321 species). These were considered 'survivors.' The 800 species in the Data Deficient (DD) category were not employed in subsequent analyses; only 5% of DD species were in the fossil record. Note that the Red List considers VU species as threatened; we decided to use only those categories at the highest risk of extinction.

We then assessed the representation of these species in three fossil databases with differing taxonomic, geographic and temporal coverage. Occurrences of Neogene mammal species were downloaded from the Paleobiology Database (Alroy *et al.* 2015). This list consisted of 53409 occurrences, representing 6049 named species and 2719 genera. Lists of fossil mammals were also obtained from the Neotoma (Neotoma 2014) and NOW (Fortelius 2013) databases. Many occurrences in these latter two databases were not unambiguously identified (*.cf.,.aff.,* ?) or included subspecies. We did not distinguish subspecies and treated occurrences in open nomenclature as valid species identifications; this had the conservative effect of increasing species counts in the fossil record. A similar process was followed for genera with 'sp' counted as a valid occurrence. A species was considered to have a fossil record if it was listed in any of the databases employed. We did not differentiate between anthropological and palaeontological collecting sites.

Species were divided into four categories: (1) not-threatened, no fossil record; (2) threatened, no fossil record; (3) not-threatened, with fossil record; and (4) threatened, with fossil record. For each, we also compiled data on body mass, geographic range and local population density. The PanTHERIA database (Jones *et al.* 2009) of life history, ecology and geography of extant, and recently extinct mammals was used to obtain estimates of local population density (number of individuals per square kilometre; number per km^2) and geographic range (area; km^2) for species in the Red List. Geographic range in PanTHERIA (variable 26-1) was based on a Mollweide projection of the total extent of a species range; data were available for 4668 species. Estimates of local population densities (PanTheria variable 21-1) were available for 956 species. Body mass (in grams) of recent and Late Pleistocene mammals were obtained from the MOM 4.0 database (Smith *et al.* 2003). This database contains body mass calculated for 4897 species, which were averaged across geographic range and gender. All available modern mammal data were log-transformed to reduce variance. We also noted the year, based on Red List data data, in which the species was formally named. We compared these properties among all species and within each of the mammalian orders used by the IUCN. Note that unlike previous studies (Alroy 1996; Barnosky *et al.* 2011), we have not omitted bats or marine mammals from our analyses.

Genera are the operational units for many synoptic palaeontological studies (Hendricks *et al.* 2014), including those that estimate ancient mammalian extinction rates (Alroy 1996; Tomiya 2013). For all species, we determined whether a member of their genus was in the published fossil record; this is equivalent to determining if a modern genus is in the record. Alternatively, if a genus consists of only species that are threatened, we considered that a 'threatened genus' and then ascertained whether it was known as a fossil.

All statistical analyses were performed using SYSTAT 13 (Systat Software Inc., Chicago, Illinois, USA.). Even after log-transformation, most variables were skewed; as a result, only non-parametric tests were used. Since we had only three variables and many cases with missing data, most comparisons were bivariate. We did perform one exploratory factor analysis (Table S3 and Fig. S1) of the combined species data, using a VARIMAX rotation of principal components to improve interpretability.

RESULTS

Of the 773 mammal species in the four most severe categories of the IUCN Red List (those we assume will be going extinct) only 68 (8.8%) were recorded in one or more of the fossil databases (Table 1). In comparison, of the 3942 species in the lower concern categories, almost an order of magnitude more (777, or 19.7%) were recorded as fossils. If we use only fossilised species, this corresponds to a future extinction magnitude of ~ 8% (68/845), compared to ~ 16% (773/4715) when all species are considered.

The proportion of not-threatened vs. threatened mammals captured in the fossil record differed significantly among orders, leading to a strikingly skewed representation (Table 2). For example, some 38.6% of all assessed cetartiodactyl species are identified in the fossil record, but only 17.9% of threatened species. For rodents, only 17.3% overall are recorded; this value fell to 4.8% for those that are threatened. Among bats, a dismal three of the 82 threatened species are recorded in the fossil record, compared to 9.9% of all species.

Species traits predict the likelihood of capture in the fossil record. As expected, for all mammals, body mass is a positive predictor of both threatened status and representation in the fossil record (Table 1 and Fig. 1a). Moreover, threatened species have larger body masses than non-threatened mammals and those found in the fossil record are larger regardless of threat status. Threatened species with a fossil record tend to be much larger than any other category. Non-threatened taxa, predictably have larger ranges than do threatened ones (Fig. 1b), but mammals with a known fossil record have wider ranges than those without a record regardless of threat status. The pattern for local population density is the inverse of body size (Fig. 1c); not-threatened species generally have larger population densities than threatened ones; mammals with a fossil record have smaller population densities for both threatened and not-threatened species. Threatened species with a fossil record tend to have the smallest local population densities. Distributions for the three variables were compared with a Kolmogorov–Smirnov two-sample test; nearly all were

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Table 1 Modern mammal species properties and their representation in the fossil record

Threat status	Number of species	Median log mass (g)	Median log population density	Median log geographic range (km^2)	Median authority year
Without fossil record					
Not-threatened	3165	1.85 (1999)	1.94 (410)	5.50 (2866)	1896 (3165)
Threatened	705	2.72 (315)	1.77 (135)	4.07 (570)	1916 (705)
All	3870	1.93 (2314)	1.86 (545)	5.30 (3436)	1898 (3870)
With fossil record					
Not-threatened	777	2.18 (719)	1.45 (280)	6.27 (709)	1832 (777)
Threatened	68	4.34 (56)	0.415 (24)	5.28 (49)	1836 (68)
All	845	2.30 (775)	1.27 (304)	6.24 (758)	1832 (845)

Threatened includes IUCN Red List™ (37) categories EX, EW, CR and EN. Not-threatened includes categories LC, VT and VU. Species with insufficient data (status DD) are omitted. Presence in the fossil record from matching species names in the Paleobiology Database, NOW and Neotoma. Mammal mass data from MOM (21), population density and geographic range from PanTheria (20). Authority year (year species description) from the Red List. Sample sizes in parentheses.

Table 2 Representation in the fossil of extant threatened and not-threatened mammals

Order	Number of species	Number of threatened species	Percent non-threatened species with fossil record (%)	Percent threatened species with fossil record (%)
Afrosoricida	50	9	0.0	0.0
Carnivora	270	38	46.1	36.8
Cetartiodactyla	267	67	45.5	17.9
Chiroptera	947	82	10.5	3.7
Cingulata	16	0	43.8	
Dasyuromorphia	70	8	12.9	25.0
Dermoptera	2	0	0.0	
Didelphimorphia	82	3	6.3	0.0
Diprotodontia	144	36	14.8	11.1
Eulipotyphla	373	60	23.3	3.3
Hyracoidea	5	0	40.0	
Lagomorpha	85	14	43.7	14.3
Macroscelidea	15	1	21.4	0.0
Microbiotheria	1	0	0.0	
Monotremata	5	3	50.0	0.0
Paucituberculata	6	0	0.0	
Peramelemorphia	19	7	16.7	14.3
Perissodactyla	16	10	100.0	70.0
Pholidota	8	4	25.0	0.0
Pilosa	10	1	11.1	0.0
Primates	408	178	6.1	3.9
Proboscidea	2	1	100.0	100.0
Rodentia	1891	248	19.2	4.8
Scandentia	17	2	0.0	0.0
Sirenia	5	1	25.0	100.0
Tubulidentata	1	0	100.0	
Total	4715	773	19.7	8.8

Threatened species are those IUCN Red List™ (19) categories EX, EW, CR and EN. Not-threatened includes categories LC, VT and VU. Species with insufficient data (status DD) are omitted. Presence in the fossil record from matching species names in the Paleobiology Database, NOW and Neotoma.

highly significantly different ($P < 0.01$; sample sizes in Table 1). The exceptions were: (1) Log geographic range, not-threatened, no fossil record vs. threatened, fossil record, $P = 0.051$; (2) Log local population densities, not-threatened, no fossil record vs. threatened, no fossil record, $P = 0.019$; (3) authority year for species description, not-threatened, fossil record vs. threatened, fossil record, $P = 0.691$. In general, these patterns also hold true for comparisons among and within orders (Table S1). If we compare species with and without a fossil record regardless of threat status, species with a fossil record were larger and have wider geographic ranges and smaller local population densities. All of these differences were significant ($P < 0.001$) using a Mann–Whitney *U*-test.

Macroecological studies have demonstrated that body mass, geographic range and local population density are all correlated; for example, in general, species with larger body mass have smaller local population density and larger geographic ranges (Brown 1995; Liow *et al*. 2008). These relationships generally hold among all four categories of species considered (Fig. 2; Table S2), most strongly the relationship between body mass and local population density (Fig. 2b). Body mass and geographic range are strongly correlated for species that are represented in the fossil record but only weakly correlated for threatened species absent from the fossil record and not correlated for non-threatened species without a fossil record.(Fig. 2a). In addition, this relationship is heteroskedastic, especially among those species that lack a fossil record; although large bodied species do not have small geographic ranges, small bodied ones can have a big or small range. This pattern also points to the dominance in the threatened list of endemic populations of small body size, such as many rodents, bats and 'insectivores' (Eulipotyphla). 'Insular' (island) species are particularly poorly represented (Fig. 3). Similarly, species that cover large areas can have large or small local population densities (Fig. 2c). At first glance, it is surprising that mammals with large local population densities are more poorly represented than those with smaller local populations (Fig. 1c). However, large local population densities are negatively correlated with both body mass and geographic range (Fig. 2b,c), indicating that these factors overwhelm the role of population density in predicting occurrence of a species in the fossil record.

An exploratory factor analysis (Table S3) of the total species data combined local population density and body mass into a single factor, with geographic range remaining separate. The two factors explained 92% of the total variance. The scores plot again suggests that geographic range is the best predictor of threatened vs. non-threatened, whereas forms with large body sizes are more likely to be in the fossil record.

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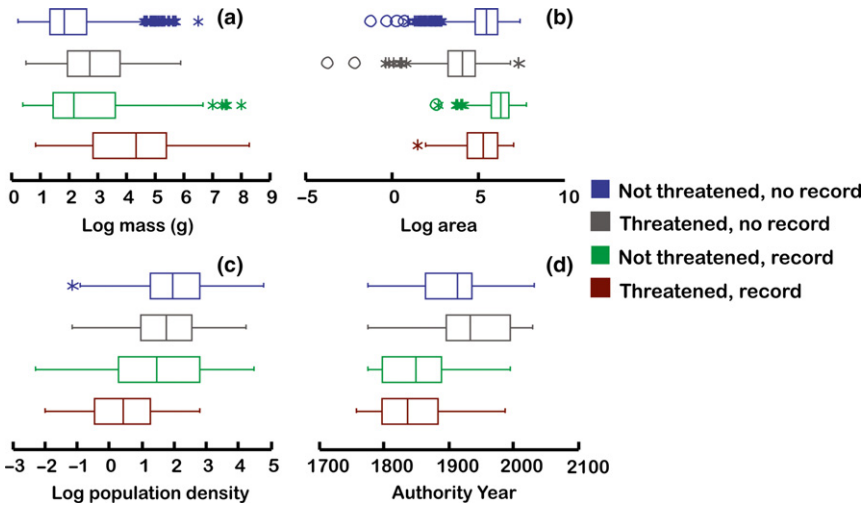

Figure 1 Box plots of properties of modern threatened and non-threatened species with and without a known fossil record. Numbers of species in each category are below each box and in Table 1. (a) Log mass (g). (b) Log geographic range (km^2). (c) Log local population densities (individual per km^2) (d) Authority year for species description. Body sizes are from (21); species geographic ranges and local population densities are from (20) Threatened includes IUCN Red List™ categories EX, EW, CR and EN. Not-threatened includes categories LC, VT and VU. Species with insufficient data (status DD) are omitted.

The year of first description of a mammal species is strongly related to its likelihood of representation in the fossil record. While those with a fossil record were mostly described in the mid-19th century (Fig. 1d, Fig. S2 and Table 1), species without a fossil record tend to have been described much later. Among species without a fossil record, threatened species are on average described more recently. The year of description is strongly related to both body size (Fig. 2d and Table 2) and geographic range (Fig. 2e); newly discovered mammals tend to be smaller and have a more limited distribution. There is no clear relationship with population density.

The fossil record for genera is markedly better than that at the species level (Table S4). Overall, nearly 40% of mammalian genera have been recorded as fossils, with ~ 58% of all species having their genus described in the record. Approximately 60% of comparatively not-threatened species have a generic record, compared to 48% for threatened species. Again, there are strong differences among orders, with good representation by carnivore and cetartiodactyl genera compared with poor representation by bats, rodents and primates (Fig. 3a). Of all modern mammal genera, 127 are comprised entirely of threatened species, for a 'real' extinction magnitude for genera of 10.7%. In comparison, if we consider only genera with a fossil record, the magnitude drops to 6.5% (26/401). Interestingly, the species/genus ratio, that is often used in converting genus rates to species rates (Barnosky *et al.* 2011; De Vos *et al.* 2015), is 3.8 for living assessed mammal species in the Red List, but rises to 5.5 when only species and genera with a fossil record are considered.

DISCUSSION

There are three independent records that document the existence of a modern mammal species. The first is the historical record based on published descriptions. Unfortunately, the rate of description of new species lags the probable rate of extinction, so that many species may disappear before they can be described (Régnier *et al.* 2015). The second potential record is archaeological; humans have sometimes created unique taphonomic conditions that preserve organisms with naturally low preservation potential (Erlandson 2013). The North American sea mink [*Neovison macrodon* (Prentiss, 1903)] became extinct before live specimens could be captured and described, but there is a record of it from Native American shell middens (Sealfon 2007). The final record is palaeontological. For example, the now extinct thylacine [*Thylacinus cynocephalus* (Harris, 1808)] although known from the historical record, is also well-known from the Pleistocene of Australia because of numerous preserved bone and skull elements (Gillespie *et al.* 1978).

Given the potentially ephemeral nature of recorded information, the very existence of species known only from the written record, let alone their extinction, may be unknown in the future. Both the archaeological and palaeontological record, in contrast, could persist if the written record is lost. Of the three types of records, only the palaeontological should be used to compare modern extinctions with those in the ancient record, since the other types are qualitatively different.

Even among already described mammals, we find only a small fraction have a fossil record. In addition, species at higher risk of extinction have about half the probability of being incorporated into the record compared to those at lower risk. The same pattern holds for genera. Viewed from the perspective of the fossil record alone, the magnitude of the current mammal 'Sixth Extinction' is thus markedly reduced. The picture may be even worse for other terrestrial vertebrate taxa. Using the same methods, but employing only the Paleobiology Database for fossil representatives, we found that only 3.3% of threatened bird species (26 out of 777) and 1.6% of threatened reptile species (9 out of 551) have a recorded fossil record.

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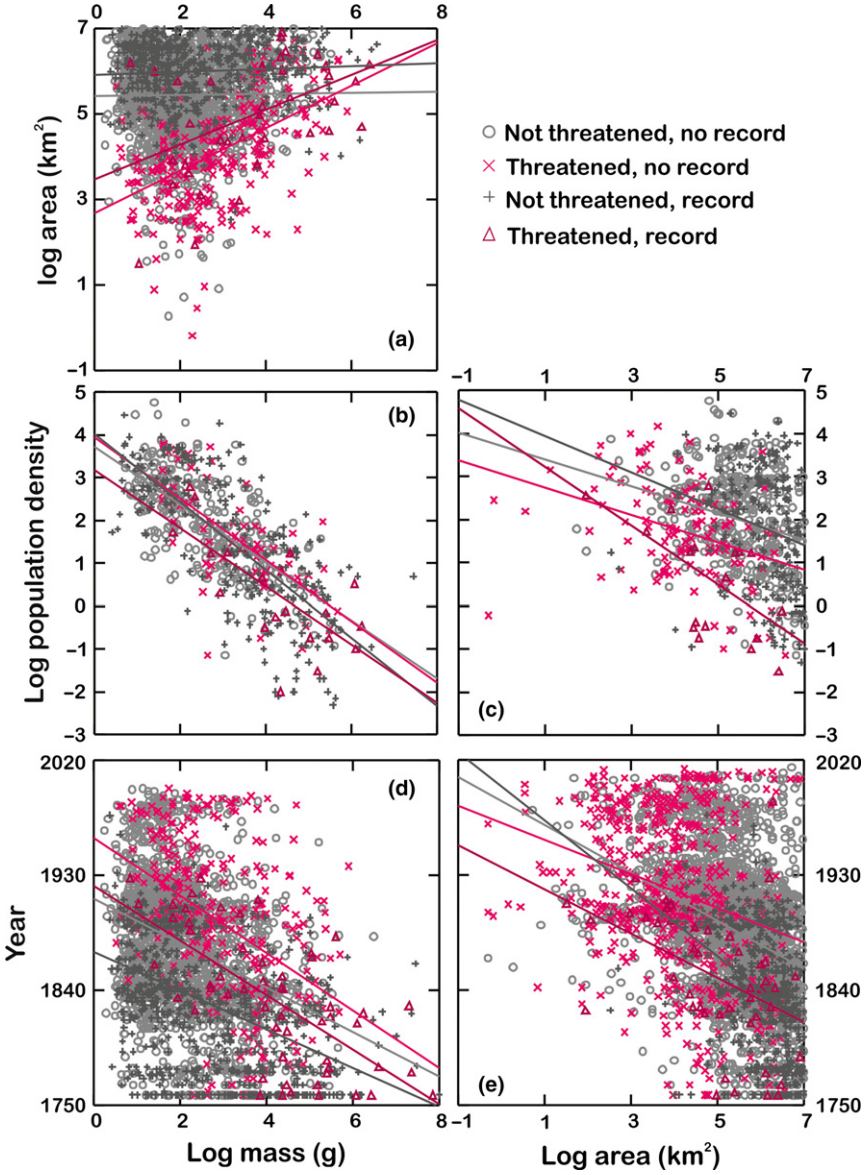

Figure 2 Comparison of properties of modern threatened and non-threatened species, with and without a known fossil record. Least square linear regression lines are shown for illustrative purposes. For each plot, sample sizes are given in parentheses in order: not-threatened, no fossil record; threatened, no fossil record; not-threatened, with fossil record; threatened, with fossil record. Correlations are given in Table S2. (a) Log geographic range (km^2) vs. log mass (g). (1937, 280, 660, 40). (b) Log population density vs. log mass (g). (296, 68, 264, 21). **(c)** Log population density vs. log range size (km^2). (381, 120, 260, 21). (d) Authority year for species description vs. log mass (g). (1999, 315, 719, 68). (e) Authority year for species description vs. log range size (km^2). (2866, 570, 709, 49).

This has direct implications for comparisons of ancient and modern extinctions. Barnosky *et al.* (2011) used a value of loss of 75% of standing crop species richness as the benchmark for comparison with the 'Big Five' extinctions and estimated how long it would take for current extinction rates to reach that value (see Ceballos *et al.* 2015). Our results suggest that actual species loss must be far higher than 75% for the modern biodiversity crisis to produce a fossilisable extinction signal comparable to the earlier mass extinctions.

We also find that some of those properties that make a species susceptible to modern extinction are correlated with those that affect their preservation potential. On average, species that are known from the record are larger and more widely distributed than those that are not. Surprisingly, they also have smaller local population densities, suggesting that the size and range are the key taphonomic variables. Species loss in earlier extinctions may thus be underestimated due to the missing record of small and endemic species (Cooper *et al.* 2006).

One intriguing result is that although there is a strong relationship between body mass and geographic range for species that are threatened, there is little or no relationship for many more species that are not-threatened, which contradicts the macroecological relationship between the two variables (Brown 1995; Smith *et al.* 2010). One possibility is that the real ecological relationship is a lack of correlation and that

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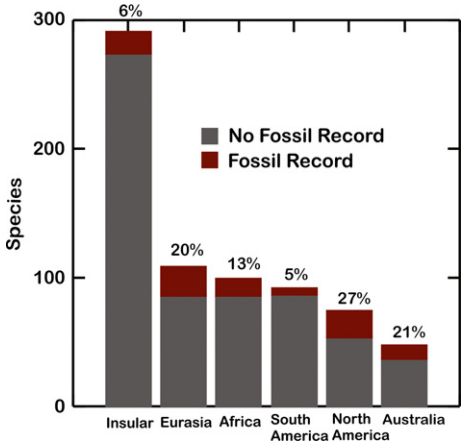

Figure 3 Number of threatened species and their representation in the fossil record by geographic region; continental areas and 'insular' (islands). Includes some species designated status DD. Total height of bars is total number of species.

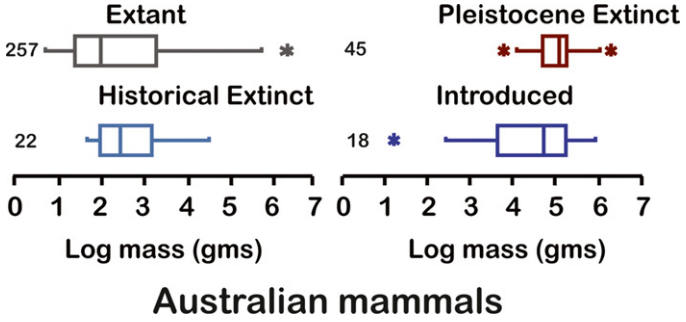

Figure 4 Body mass distributions of Australian mammals. Extant = surviving native species; Historical Extinct = species extinct in historical times; Pleistocene Extinct = species extinct prior to historic times; Introduced = non-native species currently found in Australia. Data from Smith *et al.* (2003).

the pattern for threatened species is entirely an artefact of human impacts. That is, threatened species probably have reduced geographic ranges due to human influence (Ceballos & Ehrlich 2002). The lack of a true relationship could also explain why geographic range size is typically found as a predictor of extinction risk in the fossil record, but body size often is not (Tomiya 2013; Smits 2015).

Variable preservation also affects the preserved geographic ranges of taxa, since many taphonomic variables have a strong spatial dependence (Valentine *et al.* 2006; Noto 2010). There are notable contrasts across land areas in the proportion of species with a fossil record (Fig. 3b). This suggests that taphonomic factors strongly bias preserved spatial patterns of species distribution and extinction magnitudes. We are currently developing a landscape scale model for the impact of taphonomic variables on overall preservation.

Our results also highlight potential taxonomic issues, especially the assignment of fossils to living species. We have shown that large and widespread species were generally described much earlier than small and endemic forms (Fig. 2) (Pimm *et al.* 2014). The median year of description of mammal species with a fossil record is 1834; about 80% of all mammal species have been described more recently. Very few species with a fossil record have been described since the 19th century; only 10% have been described since 1896 (Fig. 1c and Fig. S2). This may reflect a real signal: in nearly all cases a living species is named long before a fossil find was assigned to it; it should also be expected that large, widespread and abundant species should be the first to be described and that these would also be the most common fossil species. If this is the case, then the overall picture of the fossil record of living species is well-known and the measured magnitude of the current extinction based on the fossil record alone is robust. However, there may also be a tendency to assign a fossil find to the most familiar member of the recent fauna, a form of 'Pull of the Recent' (Raup 1979; Plotnick & Wagner 2006). This is supported by the high species/genus ratio for the fossil forms; fossil forms are assigned to both a familiar species and genus. Finally, it is highly unlikely that species assignments by palaeontologists will track the rapidly updated taxonomy used by mammologists, such as that used by the IUCN. Newly described living species, or subspecies raised to species rank, will almost certainly not be identified in the fossil record (Valentine *et al.* 2006). These species will thus increase the number of 'missing species' (Valentine *et al.* 2006) in the record but will not impact the magnitude measurement of the current extinction. Taxonomic revision of fossil representatives of living species may thus be needed (Prothero 2014). It should also be pointed out that genus taxonomy is likely to be more comparable and stable than the species taxonomy. Nevertheless, although the overall record is much better for genera, threatened species are still under-represented by their genera (Table S4); species taxonomy thus may not be a real issue.

Our results do not negate the reality or importance of the ongoing defaunation of the terrestrial and marine biota (Dirzo *et al.* 2014; McCauley *et al.* 2015). Rather, our goal is to highlight an overlooked problem in comparing its magnitude with that of extinctions in the past, that is, the dissimilar preservation potentials of species. A valid comparison of the magnitude of the modern extinction with the fossil record should be made by asking how the current extinction would appear if we only had the paleontological record. A comparison of rates, in particular with the iconic 'Big Five' extinctions, is also dependent on the estimates of time scales. For example, recent values for the timing of the end-Permian extinction are on the order of 60 000 years (Burgess *et al.* 2014), implying a much higher value of E/MSY than previous longer estimates, without changing the magnitude of the extinction itself. How the time scale of the modern extinction would appear in the fossil record will be the subject of future research.

Finally, we note that the future fossil record may also have a strong anthropogenic overprint. In addition to unique taphonomic conditions, major shifts in taxonomic composition are occurring, as humans and their domesticated animals homogenise local faunas (Toth *et al.* 2014). To a palaeontologist in the distant future, the extinct Australia Pleistocene marsupial megafauna would be almost instantaneously replaced by equal sized placentals (Fig. 4; Lyons *et al.* 2004) and thus be recognised as a major biostratigraphic boundary.

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AUTHORSHIP

REP, FAS and SKL collected data, REP performed the statistical analyses and wrote the first draft of the manuscript; all authors contributed substantially to revisions.

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